TWO NEW ARTHRODIRES (PLACODERM FISHES) FROM THE UPPER DEVONIAN GOGO FORMATION, WESTERN AUSTRALIA

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Two new eubrachythoracid arthrodires are described from the Late Devonian (Frasnian) Gogo Formation, Canning Basin, Western Australia. *Fallacosteus turneri* gen et sp. nov., known from a complete individual, is an advanced camuropiscid with a snout similar to that of *Camuropiscis concinnus*. It differs in the arrangement of the cheek plates, and in the proportions of the headshield, the median dorsal plate and spinal plate, and has a characteristic suborbital plate indented posteriorly to meet the marginal plate. *Fallacosteus* is placed phyletically as the sister taxon to *Tubonasus*, implying that the tubular rostra of *Rolfosteus* and *Tubonansus* are convergent features. *Pinguosteus thulborni* gen. et sp. nov., known from an incomplete trunkshield, is believed to be a coccosteoid having unusually broad, short armour devoid of dermal ornament. Functional morphology of the camuropiscids is discussed ☐ *Devonian, Frasnian, Gogo Formation, Placoderms, Arthrodire, Fallacosteus, Pinguosteus, Western Australia, Functional morphology.*

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Two new fishes from the Late Devonian Gogo Formation are described here. Relationships o the more complete form, *Fallacosteus* gen. nov., are discussed along with the functional morphology of the camuropiscid group to which it belongs. As the Gogo fishes are three-dimensionally preserved, and placoderm morphology is well-known (Miles & Dennis, 1979; Dennis & Miles, 1979a, b, 1980, 1981, 1982, 1983; Miles, 1971; Miles & Young, 1977; Young, 1984; Forey & Gardiner, 1986; Dennis-Bryan, 1987), detailed plate-by-plate descriptions of the new forms are unnecessary. Following the approach of Miles and Dennis (1979), only the salient features of these new arthrodires are described, leaving the illustrations and tables of measurements to demonstrate their general morphology. The specimens are deposited in the Western Australian Museum (WAM). Throughout the paper the words "length, breadth and height" are abbreviated to L, B, and H respectively. Abbreviations used in the illustrations are listed below.

Field work carried out at Gogo over 1986/87 produced a large number of specimens including several new taxa and much new information on previously-described species (Long 1987a, b, 1988a, b, c). Although the two new genera described here are based on single individuals only, other Gogo arthrodire genera (*Harrytoombsia, Bruntonichthys, Bullerichthys, Camuropiscis laidlawi, Simosteus, Kimberleyichthys whybrowi,*

K. bispicatus) were similarly defined on unique specimens. The range of intraspecific and intrageneric variation in arthrodires may be seen from new collections of Gogo coccosteids and *Eastmanosteus*. Observation of such variation permits determination of new genera founded upon single specimens. Because the acid-prepared Gogo material is undistorted, measurements and proportions of placoderm armour can be utilized accurately in distinguishing species, with narrow ranges for certain plate indices. Indices are here expressed as ratios of two linear dimensions multiplied by 100.

ABBREVIATIONS USED IN FIGURES

ADL	anterior dorsolateral plate
AL	anterior lateral plate
AMV	anterior median ventral plate
ASg	anterior superognathal
AVL	anterior ventrolateral plate
br.lam	branchial lamina of IL plate
CE	central plate
con	articular condyle of ADL plate
csl	central sensory-line canal groove
d.e	opening for the endolymphatic duct
lfg	inferognathal bone
ifo	infraorbital sensory-line canal groove
IL	interolateral plate

lc   main lateral-line sensory canal groove
MD   median dorsal plate
MG   marginal plate
mll   main lateral-line canal groove
mpl   middle pit-line groove
mvr   median ventral ridge of MD plate
NU   nuchal plate
AVL   area on PMV plate overlapped by
          AVL plate
oa.MG   area on SO plate overlapped by MG plate
oa.PTO   area on SO plate overlapped by
          PTO plate
P   pineal plate
PDL   posterior dorsolateral plate
pec.f   pectoral fenestra
PL   posterior lateral plate
PMG   postmarginal plate
PMV   posterior median ventral plate
PN   postnasal plate
PNU   paranuchal plate
ppl   posterior pit-line groove
pp.lam   postpectoral lamina of PVL plate
PRO   preorbital plate
PSg   posterior superognathal bone
PSO   postsuborbital plate
PTO   postorbital plate
PVL   posterior ventrolateral plate
R   rostral plate
SM   submarginal plate
smd   submedian dorsal bone
SO   suborbital plate
soa   subobstantic margin of headshield
soc   supraorbital sensory-line canal groove
so.lam   suborbital lamina of SO plate
Sp   spinal plate
vpm   vertical section of subobstantic margin of
          headshield

SYSTEMATIC PALAEONTOLOGY

Order ARTHRODIRA
Suborder EUBRACHYTHORACI
Family CAMUROPISCIDAE
Dennis and Miles, 1979

DIAGNOSIS
    As in Long, 1988a.

REMARKS
    The new genus does not possess any unusual features to warrant amendment to the familial diagnosis, recently revised in the light of the discovery of a primitive new camuropiscid, *Latocamurus* (Long, 1988a).

Genus **Fallacosteus** gen. nov

ETYMOLOGY
    Latin *fallacio*, deceit; *os*, bone. Alluding to the rostral plate which resembles that of *Camuropiscis concinnus*. The gender is male.

TYPE SPECIES
    Fallacosteus turneri sp. nov.

DIAGNOSIS
    Camuropiscid arthrodire with flat, elongate rostral plate similar to that of *Camuropiscis concinnus*; headshield B/L index of 58; preorbital plates have zig-zag median suture; suborbital plate indented posteriorly to receive an anteroventral lobe from the marginal plate; marginal plate has an extensive anterodorsal lobe below main lateral-line canal groove which almost reaches the junction of infraorbital and main lateral line grooves; postsuborbital plate overlaps marginal plate and excludes submarginal from contact with suborbital plate; median dorsal plate has strongly-indented anterior margin with total B/L index close to 66; spinal plate very short; dermal ornament of small, densely-packed pointed tubercles.

REMARKS
    The new genus resembles *Camuropiscis concinnus* in the shape of the rostral plate. It differs from *C. concinnus* by the submarginal plate not contacting the suborbital, the broader headshield, shorter spinal, broader median dorsal, proportional size of the postorbital division of the cheek (Table 2), and morphology of the suborbital and marginal plates. It may be distinguished from the other camuropiscids by the shape of the rostral plate and proportions shown in Table 2. The total B/L index stated in the diagnosis and in Table 2 refers to the maximum breadth/maximum length of the median dorsal plate, not incorporating the paramedian length given in Table 1.

Fallacosteus turneri sp. nov.
(Figs 1-3, 4, 5B, 6, 7A)

1988c *Fallacosteus turneri*; Long, p. 439, 440, fig. 3 bottom, *nomen nudum*.

ETYMOLOGY
    For Dr Susan Turner, for her role in organising the de Vis Symposium and contributions to vertebrate palaeontology.

DIAGNOSIS
    As for genus.

TABLE 1. Measurements of (in millimetres) *Fallacosteus turneri* gen. et sp. nov., Holotype WAM 86.9.697, based on the scheme of Miles and Dennis (1979).

Length of skull	67.4	Length of Ifg	30
Breadth of skull across posterolateral angles	32	Length of biting division of lfg	15
Breadth of skull across posteromedial angles	37.6	Length of trunk shield	85.5
		Breadth of trunk shield	39
Depth of skull	25	Depth of trunk shield	38.5
Prepineal length	26.4	Rostrocaudal length of flank armour	27
Length of orbit	16		
Length of NU	19.5	Length of pectoral fenestra	14
Length of lateral articular fossa	3.2	Length of MD	32.4
		Breadth of MD	26
Depth of lateral articular fossa	ca.1.8	Length of Sp	6
Angle between axis of articular fossa and dorsolateral surface of skull	250	Angle between Sp and rostrocaudal axis of armour	ca.11°
		Length of AVL	35
Length of cheek	36	Length of spinal division of AVL	17.5
Length of postorbital division of cheek	21		

HOLOTYPE

WAM 86.9.697, almost complete individual lacking only the parasphenoid, left submarginal and postmarginal plates.

OCCURRENCE

From near Long's Well (close to locality no. 55 of Miles 1971, fig. 1). Gogo Station, near Fitzroy Crossing, Western Australia; Gogo Formation, Lower Frasnian.

MEASUREMENTS

Table 1. Measurements follow points designated by Miles and Dennis (1979, figs 1-3). Proportional statements in the diagnosis along with other indices are shown with those of other camuropiscids in Table 2.

DESCRIPTION

The description of salient morphological features is given within a phylogenetic framework which assumes that because *Fallacosteus* is a camuropiscid then it is also a eubrachythoracid arthrodire possessing all the characters of this group (Dennis & Miles, 1983). The spindle-shaped armour of *Fallacosteus* is restored in lateral, dorsal, ventral and anterior views (Figs 1, 2). *Fallacosteus* is recognized as a camuropiscid by the following characters (from Long, 1988a):

(1). The rostral plate is broad posteriorly (Figs 4B, 7E), slightly broader than that in *C. concinnus* (Fig. 5A), having exactly the same outline in dorsal view as that of *Tubonasus* (Fig. 5C), and differing from the T-shape rostral plates of other coccosteoids (*sensu* Denison, 1984).

(2). The postnasal plate is deep and excludes contact between the suborbital and preorbital plates (Fig. 4A). Although the postnasal is only partly preserved, its full outline can be restored from its overlap areas on the preorbital and rostral plates (Fig. 1).

(3). The cheek unit is firmly attached to the lateral margin of the skull roof (Fig. 3; 4A). The suborbital is unique amongst camuropiscids in the shape of its dorsal margin and its indented posterior margin, and resembles *Camuropiscis* in the degree of interconnection between the cheek and skull roof (Fig. 6).

(4). The dentition is durophagous (Figs 4D-G). The toothplates closely resemble those of

TABLE 2. Comparative indices of certain morphological features in camuropiscid arthrodires. L, *Latocamurus*; C, *Camuropiscis concinnus*; R, *Rolfosteus*; F, *Fallacosteus* gen. nov., T, *Tubonasus*. (n) = number of specimens. Indices rounded to nearest whole number. Range stated where more than one specimen measured. HS = headshield, TS = trunkshield; plate names as in list of abbreviations.

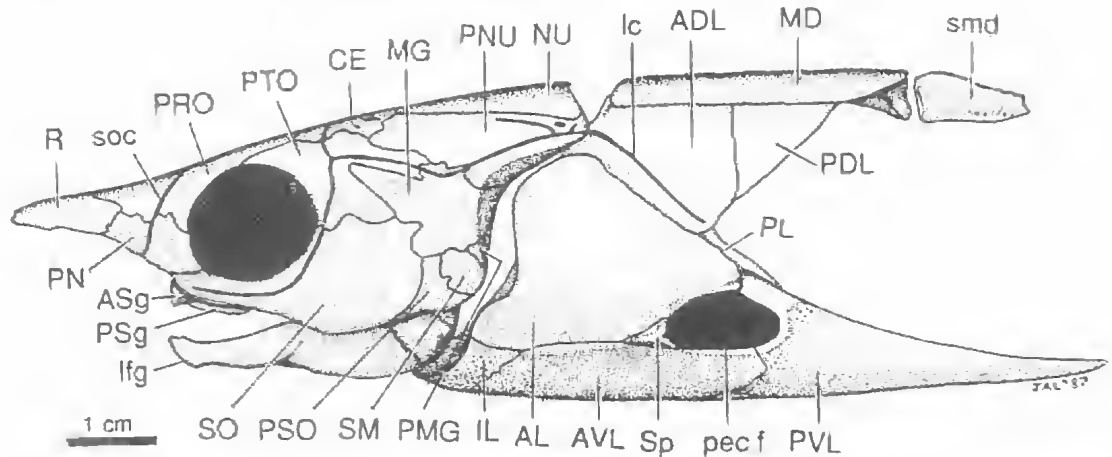|	L (1)	C (1)	R (1)	F (1)	T (2)
Headshield B/L	ca.73	48	35	58	51-55
Orbit/prepineal L HS	ca.43	42	37	39	40
Descending lamina PRO/L PRO	33	28	45	28	36
L postorbital division cheek/skull L	41	27	19	31	25-28
MD plate B/L	58	61-66	68	80	68-74
Max. L MD B/L	54	60	60	67	67
TS B/L	ca.48	46	38	46	47
Sp.L/AVL L	34	23	ca.20	17	12-13
Pect.fenestra L/TS L	20	18	18	16	16

Fig. 1. *Fallacosteus turneri* gen. et sp. nov. Restoration of dermal skeleton in lateral view, after holotype WAM 86.9.697.

Camuropiscis, *Tubonasus*, and *Rolfosteus* in having broad, flat, crushing surfaces, differing from *Latocamurus* which has broad, rounded tubercles on the upper jaw toothplates.

(5). The postsuborbital and submarginal plates are reduced in size, relative to other coccosteiods, and form a tightly-connected unit (Figs 4A, 7A). The submarginal has an indented anterior margin where it meets the postsuborbital. A subcutaneous sensory pit, seen in *Tubonasus* (Dennis & Miles, 1979b, fig. 15A) is not present.

(6). Preorbital plates have medial contact (Fig. 4B). Unlike other camuropiscids the preorbital plates form a very jagged suture along their area of contact.

(7). The postmarginal sensory-line groove is not present (Fig. 4A).

(8). The main lateral-line groove always crosses the ventral part of the anterior dorsolateral plate (Fig. 4A). This character may occur in other arthrodires (e.g. *Harrytoombsia*), but in such cases a dorsal sensory-line groove is also developed. Camuropiscids display only the ventral branch of main lateral-line canal.

Although only characters 2 and 7 are unique to camuropiscids amongst arthrodires, all of the above characters are restricted to the family within the Coccosteoidei, and thus serve to define the monophyly of the group within this narrow frame of reference. It has been suggested that camuropiscids are derived from coccosteid stock and that *Incisoscutum* serves to bridge the gap with coccosteids (Denison, 1984; Long, 1988a).

Furthermore, *Fallacosteus* is identified as an advanced camuropiscid more derived than *Latocamurus* by virtue of:

(9). A pointed rostral plate (Figs 4A, B, 7E).

(10). The postsuborbital plate is smaller, being comparable in size with that of other camuropiscids (Fig. 6).

(11). The preorbital plates have more extensive median contact (Fig. 5), differing from *Latocamurus* which has only a very short area of contact between the preorbitals.

(12). The anterior lateral plate has extensive contact with the anterior ventrolateral plate (Figs 4A, C). This synapomorphy is one of the most distinctive features of advanced camuropiscids (Denison, 1984). The anterior ventrolateral plate lacks an upturned overlap lamina for the anterior lateral, seen also in *Tubonasus* (Dennis & Miles, 1979b, fig. 13H).

Fallacosteus is considered more derived than *Camuropiscis* or *Rolfosteus* because it shares the following synapomorphies with *Tubonasus*:

(13). The postsuborbital plate contacts the marginal plate and excludes the submarginal plate from contact with the suborbital plate (Fig. 6).

(14). The spinal plate is very short (Fig. 4A), shorter than in all camuropiscids except *Tubonasus* (Table 2).

(15). The pectoral fenestra is proportionately small (Table 2).

(16). The posterior margin of the cheek unit is almost vertically oriented and is more extensive than for other camuropiscids (vpm, Fig. 6).

DISCUSSION

This phylogenetic scheme leaves *Camuropiscis* and *Rolfosteus* as the stem group to *Fallacosteus*
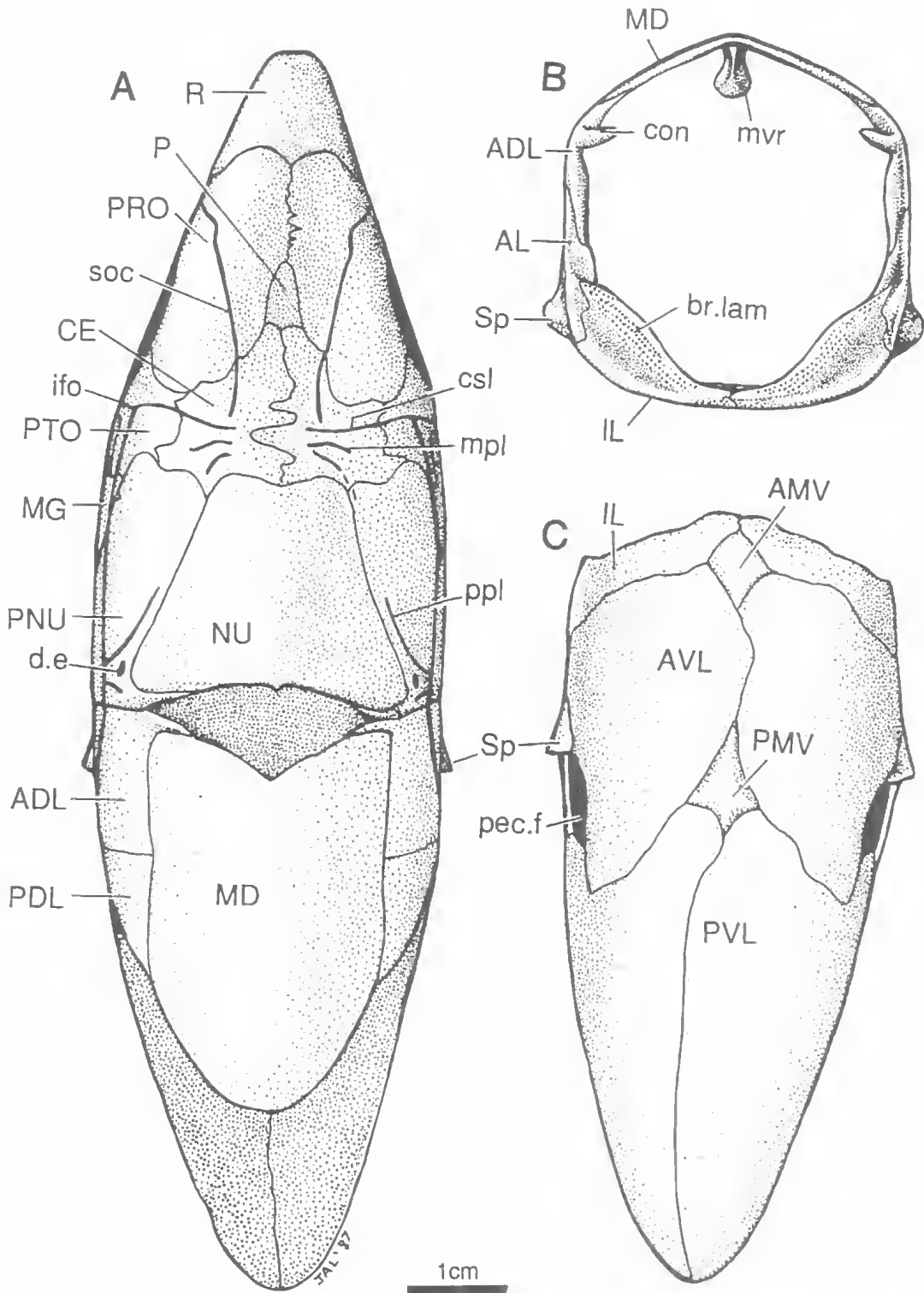
FIG. 2. *Fallacosteus turneri* gen. et sp. nov. Restoration of dermal skeleton in A, dorsal view. B, anterior view, and C, ventral view of trunkshield.
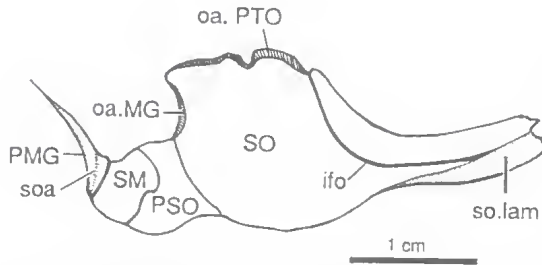
FIG. 3. *Fallacosteus turneri* gen. et sp. nov. Right cheek unit, with plates fitted together, after holotype WAM 86.9.697.

and *Tubonasus*, although there are no obvious characters uniting *Camuropiscis* and *Rolfosteus* as a distinct lineage.

In addition to these features, the following autapomorphies distinguish *Fallacosteus* from all other camuropiscids. The marginal plate has a very extensive anterodorsal lobe projecting far into the postorbital plate and almost reaching the junction of the infraorbital and main lateral-line grooves (Fig. 1). The ventral part of the marginal also projects into a concave margin on the suborbital plate (Figs 3, 4A). The holotype of *Tubonasus* shows a projection of the marginal plate into the postorbital plate, but this lobe includes the main lateral-line canal groove, whereas in *Fallacosteus* the sensory-line groove runs dorsal to the projecting lobe of the marginal plate. The dorsal margin of the suborbital plate is irregular but smooth, not sharply sutured to the skull roof as in *Camuropiscis*, but more firmly attached than for other camuropiscids (Fig. 6). The submarginal plate is indented anteriorly to receive a lobe from the postsuborbital plate (Figs 3, 4A). The preorbital plates meet in an irregular, sharply zig-zag suture. On the visceral surface of the rostral plate (Fig. 7E), a strong transverse ridge divides the anterior concave region from the flatter posterior region. The anterior region has a roughened surface, presumably for attachment of the rhinocapsular division of the endocranium.

Figs 7A-A' are a stereo pair of the visceral surface of the posterior half of the skull roof and cheek unit, showing typical features seen on other camuropiscids, such as the well-defined triangular depression on the postorbital plate (cf. Miles & Dennis, 1979, fig. 16, tri), the paired infranuchal pits, and the quadrate bone with its narrow detent process. The supraorbital vault has very weak postocular processes. The posterior face of the nuchal has only a single median process unlike the paired process of *Camuropiscis*.

The right pelvic girdle is well-preserved (Figs 4H, I), resembling closely that of *Camuropiscis* and *Incisoscutum* in approximately the same number and placement of neurovascular canals (Miles & Dennis, 1979, 1981). The girdle does differ in several points from that of *Camuropiscis*; the thickening of endochondral bone which rims the perichondral basal plate does not extend all the way around as in *Camuropiscis* but terminates at the level of the articular crest, as in *Incisoscutum*; the metapterygial articulation area is separated from the articular crest; the symphysial articulation area is posterolaterally-oriented in *Fallacosteus* instead of posteromedially-oriented as in *Camuropiscis*. If it can be assumed that the symphysial articulations had the same transverse orientation in the two genera, then the articular crest in *Fallacosteus* faced more posteriorly than in *Camuropiscis*. It appears that *Incisoscutum* had a similarly-directed pelvic girdle (Dennis & Miles, 1981, fig. 20).

The dermal ornament (Figs 4, 7A) consists of very closely-packed, high tubercles exactly as in *Camuropiscis*, being coarser than in *Latocamurus, Tubonasus* and *Rolfosteus*.

Suborder COCCOSTEOIDEI
Family indeterminate
Genus **Pinguosteus** gen. nov.

ETYMOLOGY

Latin *pinguis*, fat; *os*, bone. Alluding to the broad proportions of the armour. The gender is male.

TYPE SPECIES

Pinguosteus thulborni sp. nov.

DIAGNOSIS

A eubrachythoracid arthrodire having a very broad, short trunkshield with a posterior median ventral plate broader than long; a posterior ventrolateral plate with a short postpectoral lamina and a lateral lamina which meets the ventral lamina at $120°$; anterior dorsolateral plate is twice as deep as long, with dorsal margin shorter than ventral margin; dermal bones lack ornament.

REMARKS

Despite the paucity of material, *Pinguosteus* is readily distinguished from all other known eubrachythoracids which possess a postpectoral lamina on the posterior ventrolateral plate (buchanosteids, coccosteids, pholidosteids, camuropiscids) by its unusually broad proportions. *Harrytoombsia* has the broadest trunkshield of the known Gogo arthrodires. It has a postpectoral
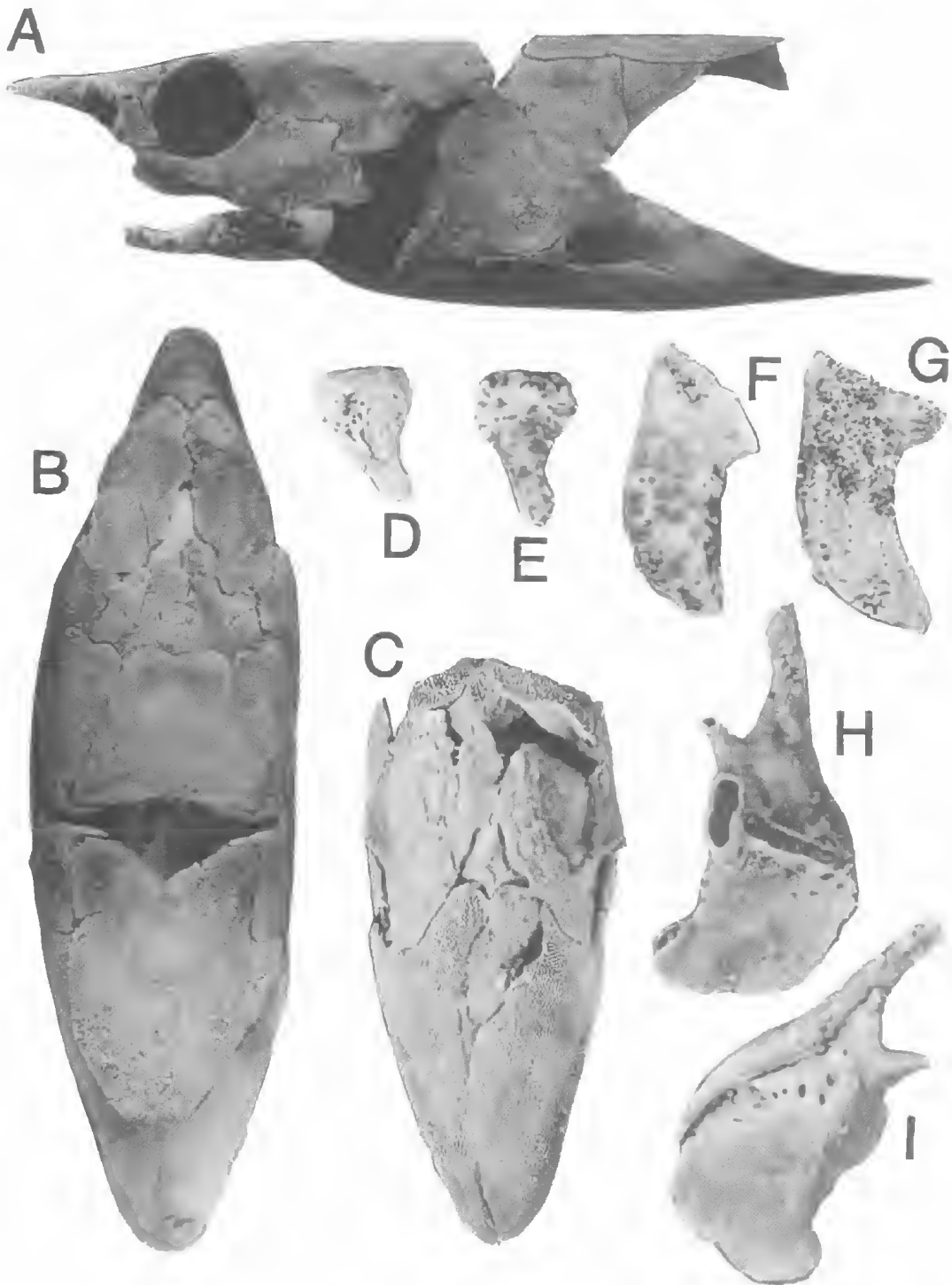
FIG. 4. *Fallacosteus turneri* gen. et sp. nov., holotype WAM 86.9.697. A, dermal skeleton in left lateral view; B, in dorsal view and C, in ventral view (trunkshield only), all natural size. D, left anterior superognathal in dorsal view. E, right anterior superognathal in ventral view. F, right posterior superognathal in ventral view. G, left posterior superognathal in ventral view (D-G, X 3). H, I, right pelvic girdle in (H) lateral view and (I) mesial view (X 3). Whitened with ammonium chloride.
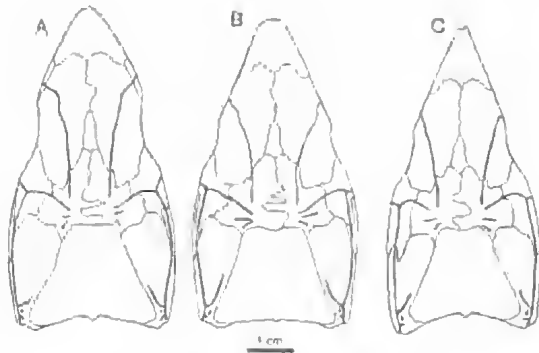
Fig. 5. Camuropiscid headshields in dorsal view. A, *Camuropiscis concinnus* (after Dennis and Miles 1979a, fig. 2); B, *Fallacosteus turneri* gen. et sp. nov.; C, *Tubonasus lennardensis* (after WAM 86.9.669).

lamina on the posterior ventrolateral plate (this excludes pachyosteomorph types such as *Eastmanosteus, Incisoscutum, Bruntonichthys* etc.), and the proportions of its trunk armour do not even closely approach that of *Pinguosteus* (Fig. 8). The absence of dermal ornament and shortness of the postpectoral lamina are further distinguishing features. I know of no other arthrodire likely to be confused with *Pinguosteus* since other broad-shielded forms either have dermal ornament or lack a postpectoral lamina (e.g. certain dinichthyids, homosteids, heterosteids; Denison, 1978).

Pinguosteus thulborni sp. nov.
(Figs 7B-D, F-I, 8A, 9B)

1988c *Pinguosteus thulborni*; Long, p. 440, *nomen nudum.*

ETYMOLOGY
For Dr Tony Thulborn, for his role in organising the de Vis Symposium and his contributions to vertebrate palaeontology.

DIAGNOSIS
As for genus.

HOLOTYPE
WAM 86.9.698, only specimen, consisting of left anterior dorsolateral, posterior ventrolateral, posterior lateral and dorsolateral plates, posterior median ventral plate, imperfect right posterior ventrolateral plate, and a small pointed bone probably from the pelvic girdle.

OCCURRENCE
Gogo Station, near Fitzroy Crossing, Western

Australia; close to locality 79 of Miles (1971, fig. 1). Gogo Formation; Lower Frasnian.

MEASUREMENTS
Posterior median ventral plate: $L = 31$ mm, $B = 32.4$ mm; anterior dorsolateral plate: $H = 31.7$ mm, $L = 16$ mm; posterior dorsolateral plate: $H = 27$ mm, $L = 19.5$ mm. Angle between ventral lamina and postpectoral lamina of posterior ventrolateral plate $= 120°$.

DESCRIPTION
As the plates are fully illustrated, the following comments deal with reconstruction of the trunk armour, an unusual, pointed bone probably from the pelvic girdle, and the dermal bone surfaces.

A small pointed bone (Figs 7B, C) referred to above, was found in association with the other remains in the same concretion. It is broad and flat at one end; the other end tapers sigmoidally to a sharp point. It lacks surface ornament or morphological features for attachment or overlap of other skeletal elements.

DISCUSSION
The armour has been restored by fitting the posterior ventrolateral and posterior median ventral plates together with the medial margin of the first plate oriented approximately parallel with the rostrocaudal axis of the body (Figs 8A, 9). As in other arthrodires, the anterior ventrolaterals are restored as marginally shorter than the posterior ventrolaterals. The anterior dorsolateral and posterior dorsolateral plates overlap to give an idea of the lateral view of the armour (Fig. 9). An unusual feature of *Pinguosteus*, not seen in other Gogo arthrodires, is that the postpectoral lamina of the posterior ventrolateral plate is entirely visible in ventral view because the lateral lamina bends upwards at $120°$, rather than at $90°$ as in most arthrodires. The specimens are not crushed or distorted, although some breakage occurred during preparation (Figs 7D, F). As reconstructed, the armour is unusually broad and short for an arthrodire with a deep profile. The broad posterior median ventral plate has a short transverse anterior margin for contact with the anterior median ventral plate.

From the asymmetry of the small pointed bone I assume it to be a paired element, not a singular intermyotomal bone, and most likely it comes from the pelvic girdle. In the pelvic girdle of *Fallacosteus* there is a stout ossification of endochondral bone around the perichondral basal plate, and it is likely that in *Pinguosteus tholborni* the endochondral rod became separated from the basal plate. It differs
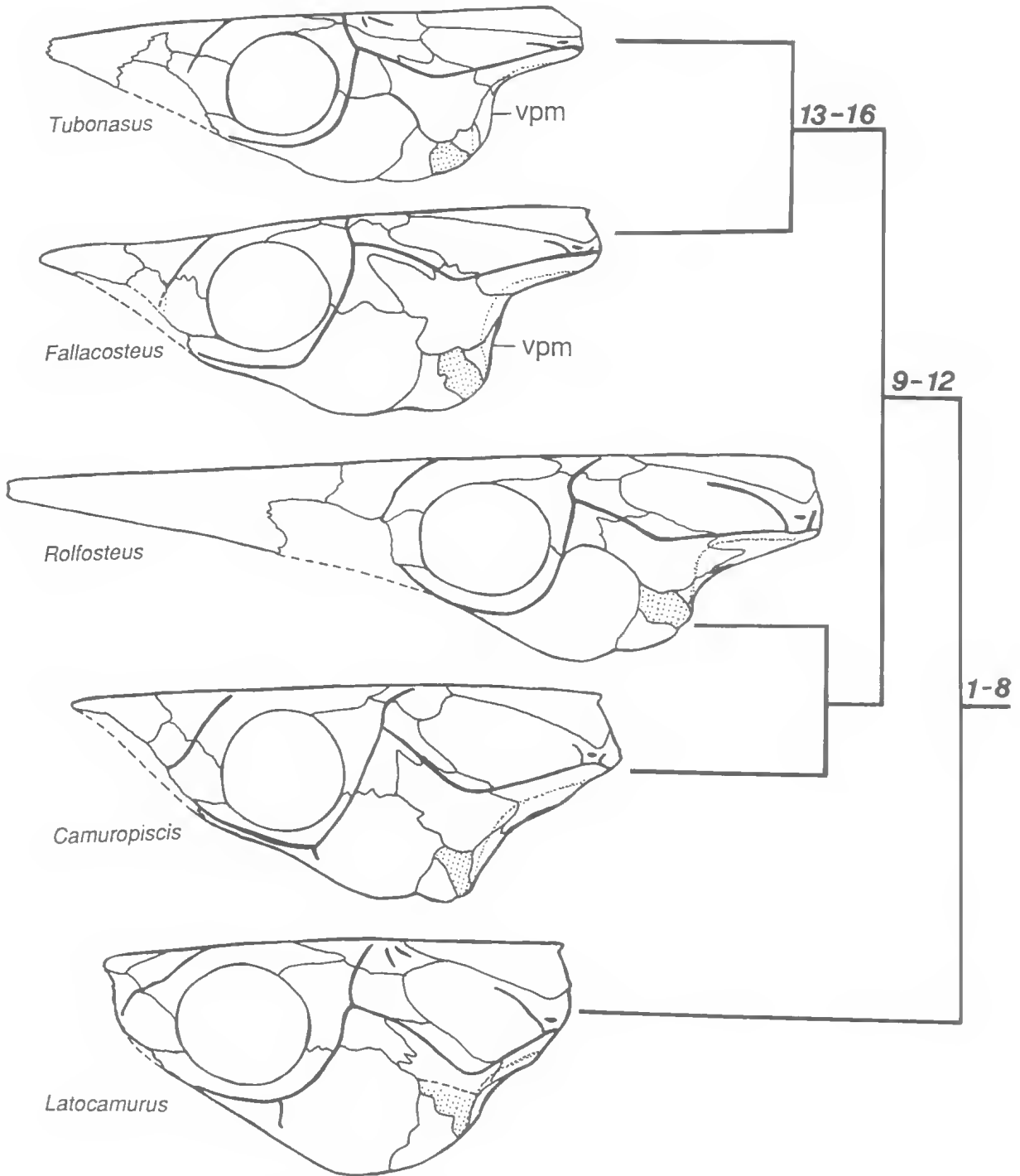
CAMUROPISCIDAE

FIG. 6. Camuropiscid headshields in left lateral view arranged in scheme of interrelationships as discussed in text. Submarginal plates stippled. Synapomorphies listed in text.
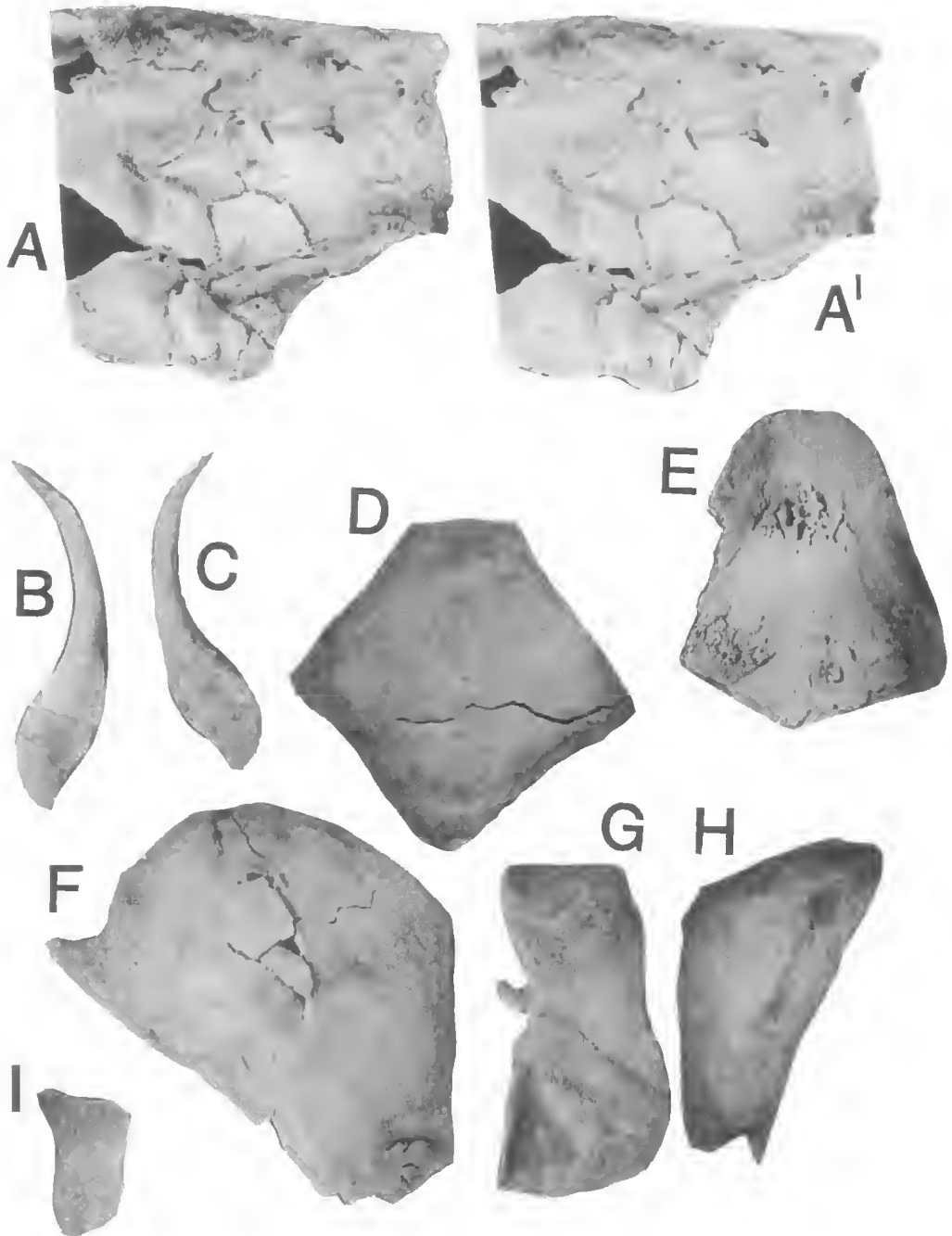
FIG. 7. A, E. *Fallacosteus turneri* gen. et sp. nov., holotype WAM 86.9.697. A, A' stereo pair showing visceral surface of right cheek and rear of skull roof (X 1.3); E, rostral plate in visceral view (X 2). B-D, F-I. *Pinguosteus thulborni* gen. et sp. nov., holotype WAM 86.9.698. B, C, possible endochondral rod from pelvic girdle in B, visceral? and C, lateral? views (X 5). D, posterior median ventral plate in ventral view; F, posterior ventrolateral plate in ventral view; G, left anterior dorsolateral plate in lateral view; H, left posterior dorsolateral plate in lateral view; I, right posterior lateral plate in lateral view (all X 1.5). Whitened with ammonium chloride.
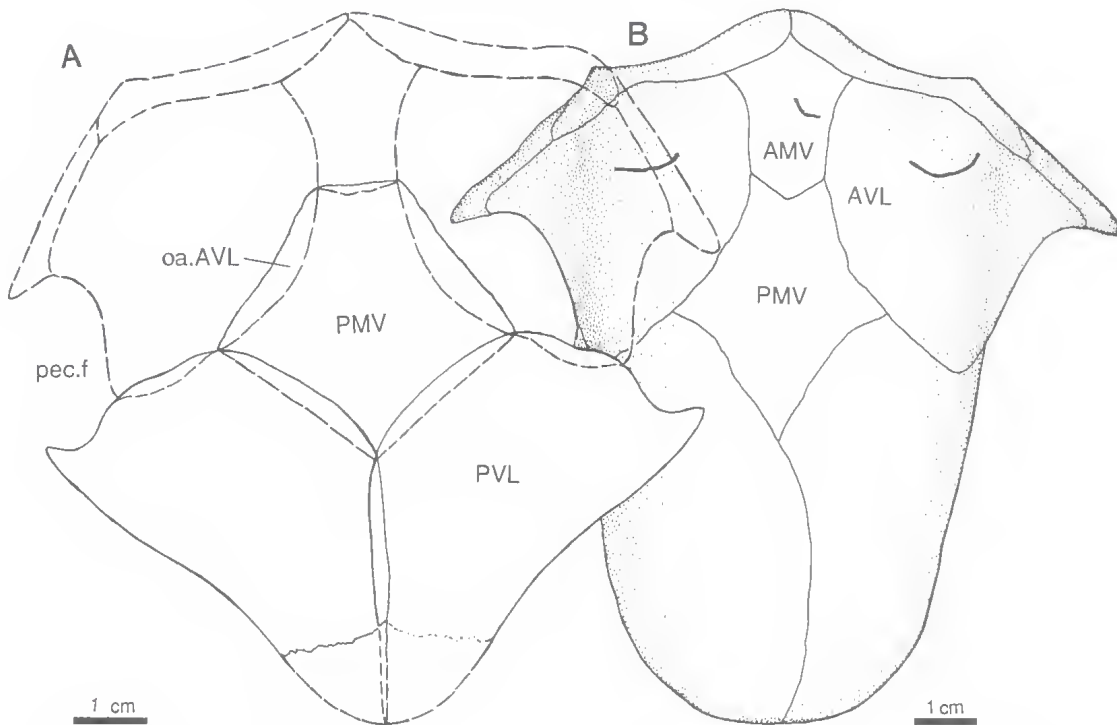
FIG. 8. Reconstructed trunkshield of (A) *Pinguosteus thulborni* gen. et sp. nov. in ventral view, compared with similar view of trunkshield of (B) *Harrytoombsia elegans* (after Miles & Dennis, 1979).

from that structure in *Fallacosteus* and *Camuropiscis* by having a broadened base. Alternatively, it could be a highly-reduced inferognathal (cf. *Homostius*), but if this were correct it resembles the inferognathal of an antiarch rather than that of an arthrodire (see

FIG. 9. *Pinguosteus thulborni* gen. et sp. nov., reconstructed trunkshield in lateral view, after holotype WAM 86.9.697.

Young, this volume). This interpretation is not supported by visible wear surfaces on the bone. As no bones from the head were found in the concretion it is likely that only the posterior part of the fish was preserved, and this favours the interpretation that this unusual element is a pelvic girdle bone. The pelvic girdle of *Holonema* contains a stout, rod-like bone with a thickened medially-directed base (pers. obs.), supporting the view that the curved, pointed bone in *Pinguosteus* is a pelvic bone.

The surfaces of the dermal bones lack tubercles or any other form of ornament. Some plates show areas of etched pitting, and it is possible that the few remains of *Pinguosteus* found in the same concretion came from the faeces of a large predator. Alternatively, the bones could have been attacked by algae or invertebrates whilst exposed on the muddy sea floor. If surface ornament was present on the plates originally there would certainly be some evidence of it after digestion, since older generations of tubercles are visible below the surface of bones (e.g. *Bullerichthys*, Dennis & Miles, 1980; *Eastmanosteus*, pers. obs.). Furthermore, the good preservation of the bone
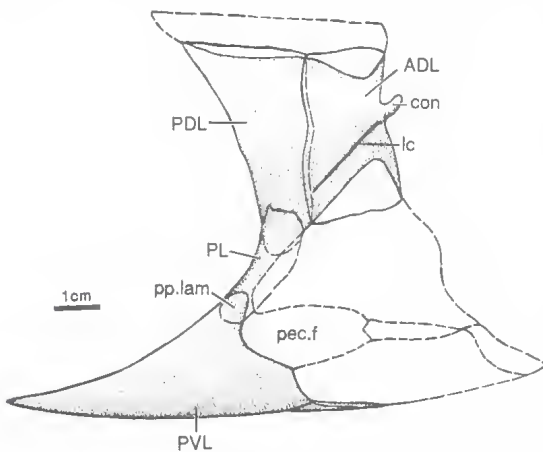
surface around the postpectoral lamina on the posterior ventrolateral plate shows the 'grain' of the dermal bone which has very fine depressions widely separated by perfectly smooth bone surface. I assume from these observations that *Pinguosteus* possessed dermal bones with smooth surfaces.

FUNCTIONAL MORPHOLOGY OF CAMUROPISCIDS

The relationships of the camuropiscids are shown in Fig. 6, based on synapomorphies listed above, and discussed by Long (1988a). From this scheme it is inferred that the tubular snouts of *Rolfosteus* and *Tubonasus* evolved independently, rather than by progression of rostral plate length from a common ancestor. This is supported by the complex arrangement of the posterior cheek regions shared by *Tubonasus* and *Fallacosteus* as well as other synapomorphies listed above. The major camuropiscid specializations (characters 1-8) have evolved in response to a durophagous diet. Thus modification of the jaw bones for crushing invertebrates or small fishes requires a firm junction between the cheek unit and the skull roof for increased pressure on the bite, and reduction in size of the postsuborbital plate which supports the quadrate and takes the most force during jaw adduction. At the anterior end of the skull the postnasal plate has been strengthened to sustain the increased pressure from the bite and brace the enlargened rostral plate. Further modifications for prey capture are seen in the very large eyes and elongation of the rostral plates and streamlining of body armour, presumably for reduction of drag when cutting through the water in pursuit of prey or escaping predators, possibly along the surface of the water as do modern sea gars (Alexander, 1967). This mode of surface-feeding would also favour the adaptation of a ventral course of the main lateral-line canal groove on the body.

Rolfosteus has the longest snout and most streamlined body armour yet retains a simple suborbital attachment to the skull roof, as does *Tubonasus*. The flat-snouted forms *Fallacosteus* and *Camuropiscis* have strongly attached cheek units, reflecting perhaps a different style of feeding which involved crushing prey of a harder nature than that eaten by *Rolfosteus* and *Tubonasus*. Possible food sources for camuropiscids could have been juvenile concavicarid crustaceans; these are commonly found as fossils in Gogo nodules and some species may have been nektonic (Briggs &

Rolfe, 1983).

Placoderms similar to camuropiscids, such as *Oxyosteus* from the Frasnian Wildungen site, Germany, are believed to have evolved their long tubular rostral plates independently because of specializations shared in the trunkshield with other brachydeiroid arthrodires (Dennis & Miles, 1979b; Denison, 1984), and because of the absence of camuropiscid synapomorphies. Similar morphological features of camuropiscids and brachydeiroids, narrow elongated armour, durophagous dentition, for example, may have resulted from both groups preying on similar crustaceans. The close faunal affinity of crustacean faunas from Gogo and central Europe has been noted by Rolfe (1966).

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